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Interspecific interactions between earthworms: A laboratory-based investigation

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Summary. Three laboratory-based experiments were undertaken to assess interspecific interactions using a range of earthworm species. These were seen as preliminary steps towards the production of mixed species populations for inoculation at land restoration sites. In the first experiment, hatchlings of 2 anecique species (*Aporrectodea longa* and *Lumbricus terrestris*) and 2 endogeic species (*Allolobophora chlorotica* and *Aporrectodea caliginosa*) were cultured in paired and single species treatments under optimal conditions for growth and survival. Growth rates of all four species were negatively affected by the presence of other species. It is proposed that the extent to which growth rates were influenced was determined by the degree of niche overlap between paired species (*e.g. L. terrestris* growth rates were most negatively affected by *A. longa*).

Experiments relating to levels of soil compaction (Experiment 2) and position of feed within the soil profile (Experiment 3) employed *A. chlorotica, L. rubellus* and *L. terrestris* (endogeic, epigeic and anecique species, respectively). In experiment 2 cocoon production was determined for the 3 species in all combinations within compacted (1.52 g cm^{-3}) or uncompacted (1.37 g cm^{-3}) soil treatments. Soil compaction significantly ($p < 0.01$) reduced *L. terrestris* cocoon production in monoculture, whilst reproductive output by *L. rubellus* was not significantly affected by compaction. Cocoon production in paired culture was not significantly affected, in both compacted and uncompacted treatments, except in the pairing of *L. rubellus* and *L. terrestris*. In this pairing *L. rubellus* cocoon production was significantly ($p < 0.01$) reduced at both soil bulk density treatments compared with the monoculture of this species. This resulted from interspecific competition for organic matter at the soil surface. In experiment 3 the effect of feed position within the soil on cocoon production was determined for various species combinations. Reproductive output was again negatively influenced by the presence of other species. The effect of feed position was species specific depending on innate feeding behaviour (*e.g. A. chlorotica* produced the greatest number of cocoons in cultures where the feed was mixed into the soil).

Key words: Cocoon, earthworms, feed placement, laboratory culture, soil compaction, species interactions

Introduction

Earthworm associations are commonly recorded and result from specific physical, chemical and biological characteristics of the soil (e.g. Nordström & Rundgren 1973; Phillipson et al. 1976; Baker 1983). Interspecific interactions may also play a role in the species composition

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of earthworm communities. Earthworm species display a range of ecological adaptations with respect to feed preference, their position within the soil profile and body size. Such adaptations may reduce niche overlap (Hutchinson 1957) and therefore allow coexistence between species (Phillipson et al. 1976; Lavelle 1983).

Negative associations between earthworms with similar ecological niches have been recorded in the field. Edwards & Lofty (1982) reported significant negative correlations between populations of *Lumbricus terrestris* and *Aporrectodea longa* and also between *Allolobophora chlorotica* and *Aporrectodea caliginosa* in agricultural plots. Replacement of native earthworms in agricultural soils by introduced lumbricid species in the Southern Hemisphere has also been recorded (e.g. Lee 1961; Reinecke & Visser 1980), although this may be due to changes in vegetation and soil to which the introduced species are better adapted (Curry 1998). A few direct, positive associations between earthworm species have also been recorded. Lukose (1960) observed a megascolecid species crawling over the giant earthworm *Drawida grandis*, which when separated always returned to the 'host' and Saussey (1957) noted that *Satchellius mammalis* was present in the burrows of *L. terrestris* and *A. longa* in a commensal association.

Few experimental studies, with the exception of Mishra & Dash (1979), Abbott (1980), Elvira et al. (1996) and Butt (1998), have had a direct focus on interactions between earthworm species. These authors assessed species interactions in terms of respiration rates, and in terms of changes in biomass and fecundity, with both intraspecific and interspecific interactions recorded. The relative strengths of interspecific interactions were found to vary between species.

This paper presents results of interspecific interactions between selected earthworm species and considers their potential role in land restoration. Laboratory-based experiments were conducted to determine if species could coexist in culture, to assess potentially mutualistic interactions between species with dissimilar ecological niches (based on the classification of Bouché (1977)) and to establish the effects of selected environmental variables, such as soil compaction and availability of feed on observed species interactions. These factors may be important in limiting the survival and spread of inoculated and indigenous earthworms at land restoration sites, where initial landscaping, uses heavy machinery which may lead to an increased bulk density of soil (e.g. Alakukku 1996). Also, restored topsoils are usually of poor quality depending on their proposed after use (Judd & Mason 1995), so organic matter may be spread on to the site to increase fertility and is therefore often found in a distinct layer, either close to or on the soil surface.

Materials and Methods

Three experiments are described which investigated the growth and reproduction of selected earthworms under a variety of conditions. Earthworms were maintained in single, paired and three species culture. Experiment 1 investigated the growth of 4 species (*A. chlorotica, A. caliginosa, A. longa* and *L. terrestris*) in paired and single species cultures under conditions for earthworm survival and growth described here as 'optimal'. In experiments 2 and 3 only three species were used (*A. chlorotica, L. rubellus* and *L. terrestris*). Here, levels of soil compaction, and feed position within the soil profile were manipulated, respectively, and interactions between the 3 species were assessed in terms of cocoon production. Individual numbers of each species were used according to the ratio of 2 *L. terrestris* : 3 *A. longa* : 4 *L. rubellus* : 6 *A. caliginosa* : 8 *A. chlorotica*. This ratio was established as a function of several factors including mean earthworm biomass, observed field densities and a requirement for viable reproduction.

All earthworms used in these experiments were produced under laboratory conditions. Experiments were conducted in darkness within temperature controlled incubators at 15 ± 1 °C (*e.g.* Lofs-Holmin 1983; Daniel et al. 1996). Culture vessels (obtained from Gregory & Co., London) were specific to given experiments, but all had sealable lids, pierced with a mounted needle to allow circulation of air. Throughout the work a pre-sterilised loamy soil (pH 6.4, organic content 5 % and moisture content 25 %) was used, which was obtained from Boughton Loam Ltd., Kettering, UK. The feed used was oven-dried, rewetted, separated cattle solids (SCS) a recognised earthworm feed, (e.g. Butt 1998) obtained from Myerscough College Farm, Lancs. These experimental conditions were considered to be "optimal" for earthworm growth, survival and reproduction.

Experiment 1: Interactions under 'optimal' conditions

Hatchlings of *A. chlorotica, A. caliginosa, A. longa* and *L. terrestris* (mean individual mass 0.09, 0.06, 0.17 and 0.08 g, respectively) were obtained from cocoons produced by laboratory-reared earthworms. Cocoons were maintained in Petri dishes on moistened filter papers at 15 ± 1 °C. On hatching, worms were transferred to 0.6 litre vessels containing a mixture of soil and SCS and kept at 5 °C until sufficient numbers were available. All hatchlings employed were obtained in the 4 weeks prior to experimentation. Treatments consisted of a monoculture of each species, all possible paired combinations plus 'double density monocultures of each species' (X2). The latter had twice the pre-determined number of earthworms per vessel. Five replicates for each of the 12 treatments were set up in 0.6 litre culture vessels (surface area 0.013 m^2, depth 0.05 m), filled to a depth of 0.04 m with soil mixed with 20 g of SCS. A further 20 g of SCS were placed on the soil surface. The total biomass for each species per pot was recorded at the outset. Thereafter the condition and mass of the earthworms was recorded monthly, at which point fresh feed was applied. The experiment was terminated after 5 months.

Experiment 2: Levels of Soil Compaction

Healthy, clitellate *A. chlorotica, L. rubellus* and *L. terrestris*, from established laboratory populations were used and all were of comparable age and condition. Two soil bulk density treatments were established, (a) non-compacted soil (bulk density 1.37 g cm^{-3}) and (b) compacted soil (bulk density 1.52 g cm^{-3}). Both soil treatments were set up in 1 litre plastic culture vessels (height 0.14 m, diameter 0.12 m). Excess SCS were applied to the soil surface of each treatment. A uniform bulk density was achieved in (a) by tapping vessels on the laboratory bench and in (b) by compacting the experimental soil in the containers utilising Standard Proctor Test equipment (Head 1980). Earthworms were initially deterred from burrowing between the edge of the vessel and the soil, as the latter had been pushed firmly against the side of the vessel.

Experimental treatments utilised paired combinations of the 3 species plus each species in monoculture, at both bulk density treatments. Two clitellate *L. terrestris*, four *L. rubellus* or eight *A. chlorotica* were introduced per treatment as appropriate. Four replicates of each of the 12 treatments were set up. Mass and reproductive condition of each individual earthworm were both recorded at the outset and at each monthly sampling, when earthworms were transferred to freshly prepared soil and fresh feed was applied. After sampling the worked soil was wet sieved through a series of graded sieves (6.7, 3.35 and 2.0 mm) and the number of cocoons produced by each species in each treatment was recorded. This experiment was terminated after 3 months.

Experiment 3: Feed Position within the soil profile

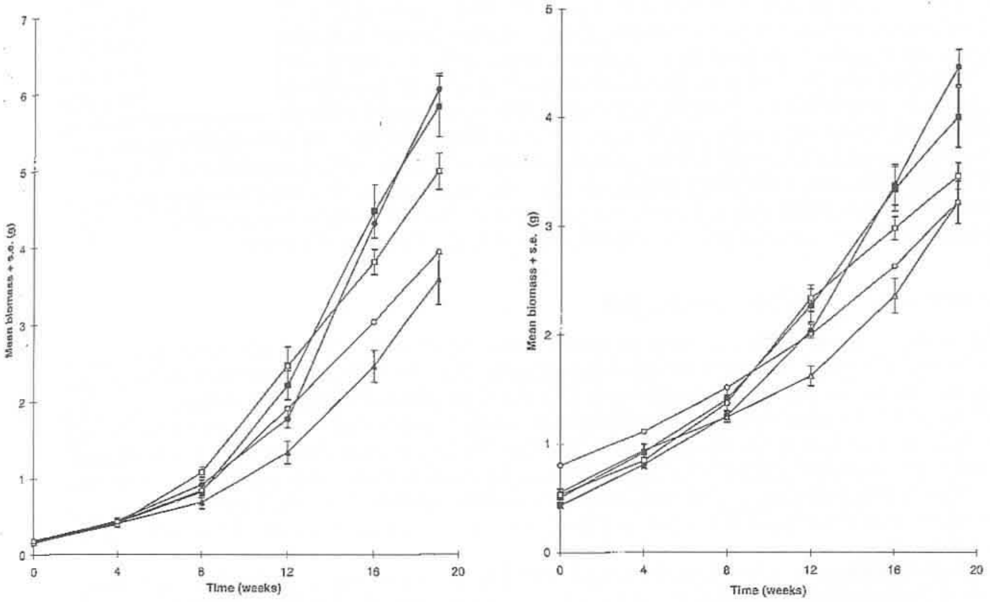
Juvenile *A. chlorotica, L. rubellus* and *L. terrestris* (initial mean masses: 0.09, 0.33 and 0.91 g respectively) were maintained in 2 litre plastic containers (surface area 0.02 m^2, depth 0.17 m) filled with soil to a depth of 0.13 m. Three feed treatments were established, each providing a total (excess) of 60 g of SCS. The position of the feed was (a) surface applied (SUR); (b) mixed into the soil profile (MIX); and (c) half (30 g) surface applied and half (30 g) mixed into the soil profile (SAM). Monocultures of the three species plus all paired combinations and a 3 species combination were established with all three of the feed treatments (SUR, MIX and SAM). Four replicates of the 21 treatments were set up.

Earthworm mass and condition were both recorded initially and at each monthly sampling thereafter, when earthworms were transferred to fresh soil. Fresh feed was applied in accordance with the experimental design. At the fourth and at subsequent samplings, the total amount of feed applied to each vessel was increased to 80 g in order to prevent this from becoming a limiting factor. Termination of this experiment took place after 6 months. The soil from the 4th, 5th and 6th sampling periods was wet-sieved as for experiment 2 and cocoon number was recorded.

Results

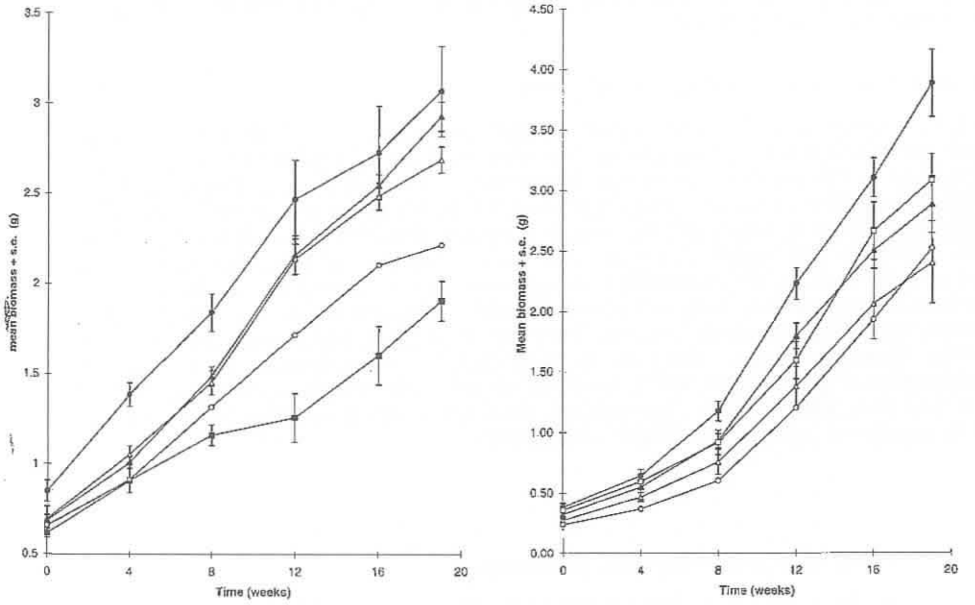
Experiment 1: Interactions under 'Optimal' conditions

Figure 1 (a–d) illustrates growth of four species over a 20 week period during which all exhibited 100 % survival and showed an increase in mass. Monocultures of all 4 species achieved the highest mean biomass-per-pot, compared (species for species) with mixed cultures (e.g. *A. chlorotica, A. caliginosa, A. longa* and *L. terrestris* growth rates in monoculture were



(a) *L. terrestris*

(b) *A. longa*



(c) *A. chlorotica*

(d) *A. caliginosa*

Fig. 1 (a–d) Growth of selected earthworm species in paired and single species culture over a 20 week period. (–●– monoculture, –■– plus *A. caliginosa*, –□– plus *A. chlorotica*, –▲– plus *A. longa*, –△– plus *L. terrestris*, –○– X2 = double the earthworm density of each of the 4 species monocultures)

0.014, 0.029, 0.067 and 0.15 g worm^{-1} week^{-1}, respectively). To enable comparisons with other treatments total pot biomasses for the X2 treatments have been halved. Growth rates for *L. terrestris* (Fig. 1a) and *A. longa* (Fig. 1b) in all paired combinations exhibited similar trends. *A. caliginosa* had the least negative effect on growth rates of other species followed by *A. chlorotica*, with the lowest growth rates in treatments where *A. longa* and *L. terrestris* were paired together (0.085 and 0.044 g worm^{-1} week^{-1}, respectively). *A. chlorotica* growth rates (Fig. 1c) were most negatively affected in the pairing with *A. caliginosa*, although *L. terrestris* had the greatest negative effect on *A. caliginosa* (Fig. 1d). For all four species, doubling the initial hatchling number greatly reduced growth rates to a level comparable with the most negative species pairings. For *A. caliginosa* growth rates of the X2 treatment were very similar to those of *A. caliginosa* in the pairing with *L. terrestris* (0.019 and 0.018 g worm^{-1} month^{-1}, respectively).

Experiment 2: Levels of Soil Compaction

Cocoon production by *A. chlorotica, L. rubellus* and *L. terrestris* in all species combinations and at the two soil bulk density treatments is illustrated in Fig. 2 (a–c). *L. rubellus* and *L. terrestris* maintained reproductive condition in all treatments and produced cocoons throughout the 12 week period.

In compacted soil treatments *A. chlorotica* was restricted to the surface layers whilst *L. rubellus* was found only within the organic matter at the soil surface. At sampling, *L. terrestris* was often found on the soil surface unattached to a burrow. Any *L. terrestris* burrows present were limited to the edges of the vessel. In non-compacted treatments *L. terrestris* was found in vertical burrows within the soil. *L. rubellus* and *A. chlorotica* were also found throughout the soil profile, with *L. rubellus* predominantly in the SCS layer at the surface.

Statistical comparisons of *A. chlorotica* cocoon production (Fig. 2a) were not possible due to a loss of reproductive condition after time of first sampling. However, certain trends are evident from the first sampling (week 4). In *A. chlorotica* monoculture, cocoon production was reduced by more than half in compacted, compared with uncompacted treatments (0.4 and 0.9 cocoons worm^{-1} month^{-1}). In compacted treatments, *A. chlorotica* cocoon production was greatest in the pairing with *L. terrestris* (0.7 cocoons worm^{-1} month^{-1}) whilst production in monoculture and in the pairing with *L. rubellus* were very similar. In uncompacted treatments the presence of *L. rubellus* reduced *A. chlorotica* cocoon production (0.5 cocoons worm^{-1} month^{-1}) in comparison with the monoculture and pairing with *L. terrestris*.

L. rubellus cocoon production (Fig. 2b) was not significantly ($p > 0.05$) affected by compaction in any treatment. In species pairings, *L. terrestris* had a significantly ($p < 0.01$) negative effect on *L. rubellus* cocoon production compared with *L. rubellus* monoculture in both compacted and non-compacted soil. *A. chlorotica* did not have a significant effect ($p > 0.05$) on *L. rubellus* cocoon production in either soil treatment. In *L. terrestris* monoculture (Fig. 2c) compaction significantly ($p < 0.01$) reduced cocoon production. *L. rubellus* and *A. chlorotica* had no significant effect on *L. terrestris* cocoon production in both soil treatments.

Experiment 3: Feed Position within the Soil Profile

During this experiment both *A. chlorotica* and *L. rubellus* became clitellate (average growth rates in monoculture were 0.012 and 0.019 g worm^{-1} week^{-1}, respectively). Cocoon production by both of these species, in all combinations and across feed treatments is illustrated in Fig. 3 (a and b). *L. terrestris* (average monoculture growth rate of 0.12 g worm^{-1} week^{-1}) did not reach maturity during the experimental period and therefore cocoon production could not be assessed for this species.

Monocultures of *A. chlorotica* and *L. rubellus* produced significantly ($p < 0.05$) more cocoons worm^{-1} month^{-1} than in paired or 3 species cultures in all feed placement treatments. In *A. chlorotica* monocultures feed position significantly affected cocoon production: MIX,

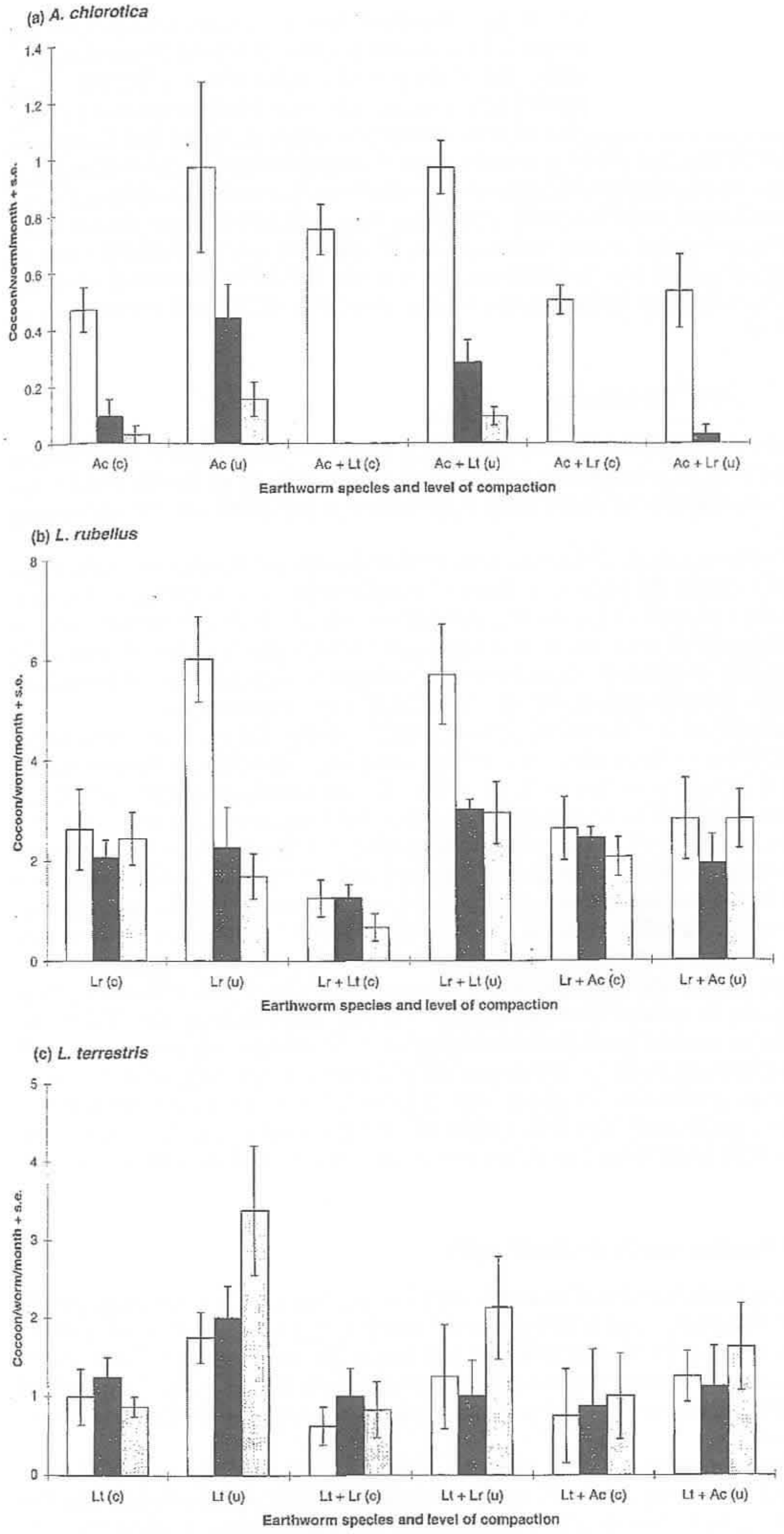
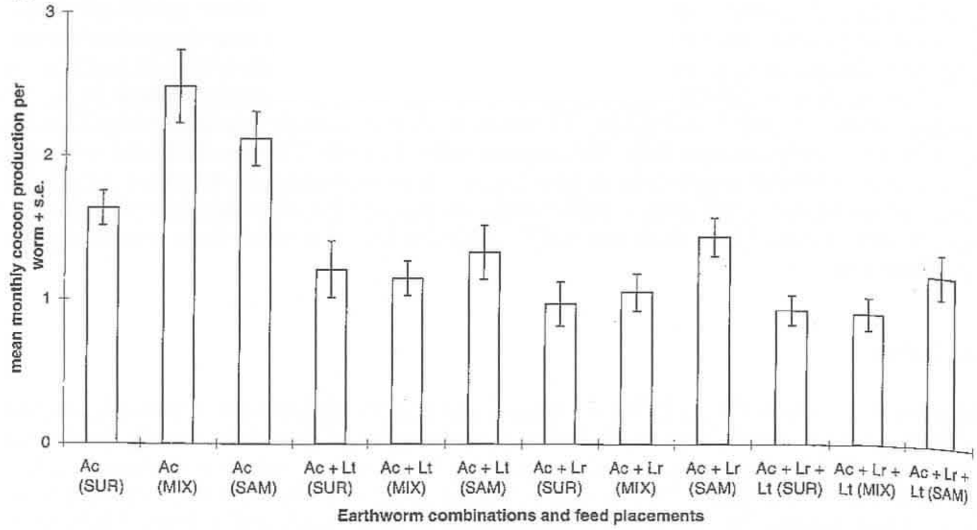

(a) *A. chlorotica*
Cocoon/worm/month + s.e.
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Ac (c)
Ac (u)
Ac + Lt (c)
Ac + Lt (u)
Ac + Lr (c)
Ac + Lr (u)
Earthworm species and level of compaction
(b) *L. rubellus*
Cocoon/worm/month + s.e.
8
6
4
2
0
Lr (c)
Lr (u)
Lr + Lt (c)
Lr + Lt (u)
Lr + Ac (c)
Lr + Ac (u)
Earthworm species and level of compaction
(c) *L. terrestris*
Cocoon/worm/month + s.e.
5
4
3
2
1
0
Lt (c)
Lt (u)
Lt + Lr (c)
Lt + Lr (u)
Lt + Ac (c)
Lt + Ac (u)
Earthworm species and level of compaction

Fig. 2 (a–c)

(a) *A. chlorotica*



(b) *L. rubellus*

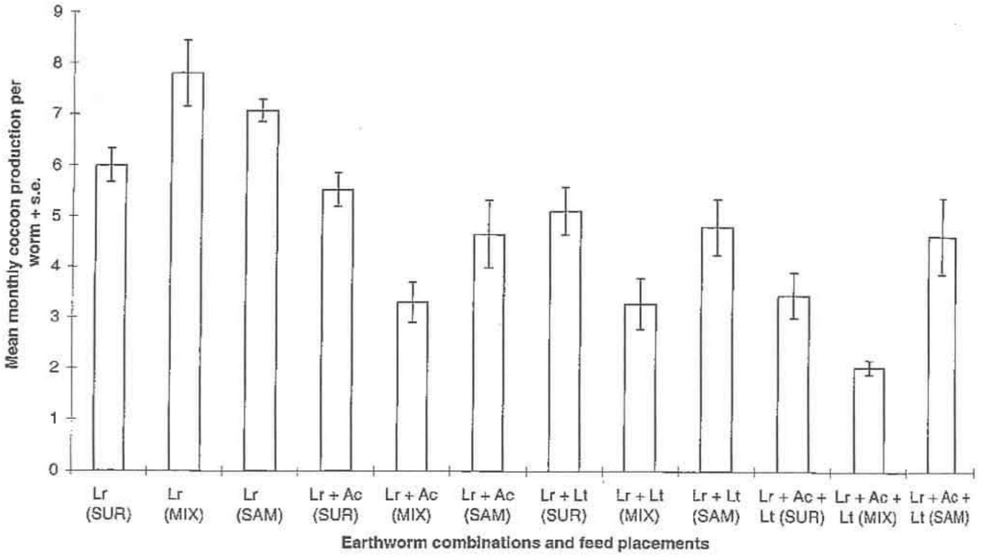


Fig. 3 (a & b) Cocoon production of *A. chlorotica* and *L. rubellus*; in single species culture; paired with each other and also with *L. terrestris*; and in three species culture with three types of feed placement. (Ac – *A. chlorotica*, Lr – *L. rubellus*, Lt – *L. terrestris*; (SUR) surface fed, (MIX) feed mixed into the substrate, (SAM) surface and mixed fed)

◄

Fig. 2 (a–c) Cocoon production of 3 earthworm species in paired and single species culture with 2 levels of soil compaction. (Ac – *A. chlorotica*, Lr – *L. rubellus*, Lt – *L. terrestris*; ☐ week 4, ■ week 8, ▨ week 12; (c) – compacted soil, (u) uncompacted soil)

2.5 cocoons worm^{-1} month^{-1} ($p < 0.01$) and SAM, 2.1 cocoons worm^{-1} month^{-1} ($p < 0.05$) were significantly greater than SUR, 1.7 cocoons worm^{-1} month^{-1}. Within paired and 3 species treatments there was no significant difference in *A. chlorotica* cocoon production between feed placement treatments. In *L. rubellus* monocultures the effect of feed position on cocoon production was similar to that shown in *A. chlorotica* monocultures where; MIX, 7.8 cocoons worm^{-1} month^{-1} and SAM, 7.1 cocoons worm^{-1} month^{-1} produced significantly ($p < 0.05$) more cocoons than SUR, 6.0 cocoons worm^{-1} month^{-1}. This pattern was not found for *L. rubellus* cocoon production in paired and 3 species treatments. In paired treatments with *L. terrestris* and *A. chlorotica*, MIX treatments produced significantly ($p < 0.05$) less cocoons worm^{-1} month^{-1} than SUR and SAM treatments between which there was no significant difference.

Discussion

Growth curves in experiment 1 (Fig. 1) suggest that all four species were negatively affected by the presence of other species in the enclosed environment of the culture vessels. This could have resulted from increased resource competition for space and organic matter compared to species monoculture. The extent to which species compete is dependent on the degree of niche overlap which they demonstrate. Growth rates of *L. terrestris* and *A. longa*, both anecique species that feed on organic matter at the soil surface, were most negatively influenced when paired together. The growth rates of *A. longa* and *L. terrestris* were influenced less in pairings with the geophagous species *A. chlorotica* and *A. caliginosa*. In such pairings, species exhibited a degree of niche separation in terms of feeding behaviour, this reduced encounter rates and competition for the fixed amount of organic matter which may have become limiting as biomass increased. We propose that intraspecific competition (as represented by X2 treatments) had a negative influence on all four species, reducing growth rates to levels comparable with those exhibited in pairings between species from the same ecological grouping. Individuals from the same species occupy identical niches and therefore competition for resources is intense within the fixed non-replenishing environment of the experiment. Butt (1998) conducted a similar laboratory experiment investigating the growth of five earthworm species (including *A. chlorotica, A. longa* and *L. terrestris*) in paired species culture. As in the current study, monocultures exhibited the highest growth rates. In paired species growth rates were most negatively affected by species exhibiting similar resource requirements. Results also complement field observations by Edwards & Lofty (1982) who reported negative correlations between *L. terrestris* and *A. longa* and also between *A. chlorotica* and *A. caliginosa* populations.

In experiment 2 soil compaction significantly reduced *L. terrestris* cocoon production in monoculture compared to the non-compacted soil treatment. In compacted soils burrow formation is restricted (e.g. Kretzschmar 1991) and in such situations energy may be diverted from cocoon production. Compaction had no significant effect on the fecundity of *L. rubellus*, an epigeic species, tending to live in the upper organic layers. Therefore, given an adequate organic layer (to prevent desiccation) this species is little affected by soil compaction. In this experiment, feed was only applied at the surface and was therefore not easily accessible to endogeic species such as *A. chlorotica* and probably contributed to the loss of reproductive condition of this species, which was compounded in compacted soil treatments. Individual species cocoon production in paired culture was not significantly affected in both compacted and non-compacted soil treatments except in the pairing of *L. rubellus* and *L. terrestris*. In this pairing *L. rubellus* cocoon production was significantly reduced ($p < 0.05$) in both soil bulk density treatments. The three species utilised in this experiment represent the 3 established earthworm groupings. These species are spatially separated within the soil profile which should limit negative interactions, however, both *L. rubellus* and *L. terrestris* consume organic matter at the soil surface and this may have resulted in interspecific competition for feed and led to a reduction in cocoon production.

Interpretation of results from experiment 3 is complex due to the large number of treatments, however, certain observations can be made. Fig. 3 suggests that cocoon production by *L. rubellus* and *A. chlorotica* can be negatively influenced by the presence of other species and also by the position of feed within the soil profile. In single species culture, *A. chlorotica* exhibited the greatest cocoon production in the MIX feed treatment reflecting this species' endogeic classification. This pattern was not evident in paired and 3 species cultures where feed placement appeared to have little influence on A. chlorotica fecundity. It is proposed that competition for the feed resource in MIX and SAM treatments (where both *L. rubellus* and *L. terrestris* were forced to feed within the soil) decreased cocoon production to the level experienced in SUR treatments, where the major factor influencing *A. chlorotica* fecundity was the lack of available organic matter. Hughes et al. (1994) conducted a field experiment in S. Australia, and investigated the effect of feed particle size and placement on earthworm numbers and cocoon production. Manure was either surface applied or evenly dispersed within the soil profile in bags of soil placed in pasture. Total earthworm numbers were not significantly affected by either feed particle size or placement, however, cocoons of *A. caliginosa, Aporrectodea rosea* and *Aporrectodea trapezoides* (endogeic species) were more abundant in bags where the feed was milled and evenly dispersed. This supports observations in *A. chlorotica* monoculture, where the MIX fed treatment produced the largest number of cocoons.

In *L. rubellus* monocultures MIX treatments also produced significantly ($p<0.05$) more cocoons than SAM or SUR treatments, not the expected result, given the surface feeding behaviour of *L. rubellus*, and is something which suggests further investigation. In paired and 3 species cultures, a pattern was evident in line with perceived *L. rubellus* feeding behaviour. MIX treatments had a significantly negative effect upon *L. rubellus* fecundity, probably resulting from increased competition for a more limited and scattered food resource.

In all three feed treatments *L. rubellus* and *A. chlorotica* cocoon production, in paired and 3 species culture, was significantly reduced compared with monocultures. This could be a result of increased earthworm density, resulting in a heightened level of resource competition between species. Encounter rates also increase with density, which will increase disturbance during copulation and cocoon deposition. Earthworms (*L. terrestris*) have been shown to interfere with mating of conspecific pairs (Nuutinen & Butt 1997) and this may also occur between species.

Preliminary work (e.g. Scullion 1992; Judd & Mason 1995) has suggested that the use of selected earthworm species introduced into reclaimed soils, can give rise to improved soil properties. The three experiments described in this current work indicate that the presence of other species under enclosed laboratory conditions can have a negative effect on growth and fecundity. It is suggested that the extent to which species interact in this way is dependent on the degree of niche separation. The influence of soil bulk density and feed position is species specific relating to behavioural and physiological characteristics. Depending on site conditions, it is proposed that the combination of selected earthworm species may be the critical factor determining the establishment of viable communities at restoration sites.

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